Differentiating Roles of Improvisational and Non-Improvisational Music Training in Resting State Functional Connectivity

By

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Chapter 1. Musicality as a Selective Spandrel

Governed by Neural Synchrony

This Chapter is adapted in part, with permission, from an essay written for Dr. Ann Burke as a part of my graduate coursework.
The capacity for musical behaviors is one of the few traits that is considered to be universally human (Brown, 1991). Every known human culture has some form of musical tradition, and the earliest musical instruments within the fossil record date back over 35,000 years (Conard, Malina, and Münzel, 2009). However, the lack of obvious survival advantages conferred by musicality has led to significant debate as to why musicality originated within human societies, and how precisely humans gained the mental capacity for the processing of musical information.

Earliest ponderings of music and evolution date back to Charles Darwin (1896), who in *The Descent of Man* referred to man’s ability to produce and enjoy music as “ranked amongst the most mysterious with which he is endowed” (p. 570). To the best of Darwin’s reckoning, musicality originated through sexual selection for the ability to mimic emotionally salient auditory stimuli, suspecting the adaptational relevance of human musicality was similar to that of the mating displays seen many songbirds (Darwin, 1896). This would become the first of many adaptationist theories suggesting that musicality evolved as a specific selective behavior. Other, more recent adaptationist theories suggest that musicality may have developed out of the exaggerated and tonal communication behaviors exhibited by parents to their young offspring (Dissanayake, 2000), or as a mode of promoting group cohesion in the earliest human societies (Roederer, 1984).

In general, adaptationists have recognized that there are many similarities in the neural processing of musical information and language (Roederer, 1984), and Darwin believed that early musical behaviors in humans predated and may have even
led to the development of language (Darwin, 1896). However, Steven Pinker (1997) argued that the connection between musicality and language could be explained in a different way, suggesting that musicality is no more than a highly decorative spandrel formed by stimulation of language and several other processing pathways within the brain. To him, “music is auditory cheesecake, an exquisite confection crafted to tickle the sensitive spots of... our mental faculties” (Pinker, 1997, p. 534). Pinker would view the perspectives of the adaptationists as overly panglossian (Gould & Lewontin, 1979), believing that music was not a specifically adaptive behavior, but instead one of the earliest human inventions.

Recognizing this debate between adaptationist and nonadaptationist theories, Aniruddh Patel (2010) sought to explore the evolutionary origins of musicality by looking directly at the brain. He established a null hypothesis based on Pinker’s theory, reasoning that if musicality were merely an artifact of other brain systems, there would not be any brain areas that have the specific function of processing musical information (Patel, 2010). He identified two behaviors that are seemingly specific to musicality, tonality processing and entrainment to musical beat, and in both of these cases he failed to find sufficient evidence to refute this null hypothesis (Patel, 2010). In the case of tonality processing, he cited the “shared syntactic integration resource hypothesis,” which suggests that musical tonality and linguistic syntax are processed by the same neural systems accessing different knowledge bases in long-term memory (Patel, 2003). As for Entrainment to musical beat, Patel noted that other animals that have exhibited vocal learning behavior, but not natural
entrainment to beat, such as parrots, have the ability to entrain to a musical beat under experimental conditions (Patel, 2009).

Failing to find any direct evidence of musicality specific brain processing regions, Patel, like Pinker, concluded that musical behaviors were most likely invented rather than evolved (Patel, 2010). However, whereas Pinker (1997) dismissed music as a mere “pleasure technology” (p. 525), Patel (2010) viewed it as a “transformative technology of the mind” (p. 2). Patel recognized tangible behavioral and neural benefits to language processing conferred by learning music at a young age (Moreno 2009), as well as therapeutic uses of music through listening paradigms in stroke patients (Särkämö et al, 2008) and musical intonation therapy in aphasics (Norton, Zipse, Marchina, & Schlaug, 2009). Patel (2010) also recognized several possible reasons why music would reach ubiquity within human populations, citing both the emotional power of music and its usefulness in group rituals and as a mnemonic device.

From the perspective of Darwin or Pinker, musicality and language are like the proverbial chicken and egg. One must predate the other, and the ultimate adaptive value is determined simply by which came first. It is of course worthwhile to explore the evolutionary roots of musicality, but the strict dichotomization of adaptationist and nonadaptationist theories falls into the fallacy that evolution occurs as discrete historical events. In an update to his theory, Patel (2018) recognized the potential role of gene culture coevolution in regards to musicality. Here, he suggests that musicality may be more akin to fire, an ancient human invention that has since shaped the course
of natural selection within humans (Wrangham, 2009). Put another way, even if musicality initially came about as a spandrel of other processing pathways, it could serve as a “selective spandrel”, and given the ubiquity, longevity, and usefulness of musical behaviors, it follows that humans would continue to develop increased specialization for musicality throughout the full course of evolutionary history, continuing even to the current day.

This conception of the evolutionary history of musicality differs from traditional adaptationist models in that it does not make the claim that musicality necessarily originated for a single ultimate purpose. In the titular example of their critique of the adaptationist program, Gould and Lewontin (1979) point to the ornately designed spandrels found within domed cathedrals as a metaphor for the prevalent assumption at the time that all observed characteristics of an organism must be selected for a specific purpose. Spandrels are a necessary structural aspect of any domed structure, so to claim that the structure was designed from the beginning with these ornate spandrels in mind would “invert the proper path of analysis” (Gould & Lewontin, 1979, p. 148). That is to say, some traits may be a byproduct of architectural necessity, and in this case one should not assume that such a trait is necessarily adaptive.

However, this is not to say that all spandrels are necessarily non-adaptive either. For example, some domed structures are built in such a way that one can whisper into one spandrel, and the same sound could then be heard in the opposing spandrel. Since spandrels are a necessary aspect of domed structures, it is likely that
the first of these “whispering galleries” (Rayleigh, 1910) were discovered by accident. Nonetheless, future architects were then able to design structures with the specific goal of promoting this natural acoustic phenomenon. In this same way, it is possible to accept that proto-musicality originally may have originally formed as a byproduct of the necessary interactions of other developing brain systems, while still holding that, as these early musical behaviors proved to have a variety of selective advantages, the neuro-architectural underpinnings promoting these interactions would have continued to evolve in order to accommodate the development of more complex musical behaviors and processing mechanisms.

Following this idea of musicality as a selective spandrel, the neural underpinnings of musicality would not be defined by the actions of a single brain area, but rather in the way brain areas communicate. One potential mechanism of neural communicability relates to an interesting phenomenon in physics, in which asynchronous metronomes on a free moving base will spontaneously synchronize with one another (Pantaleone, 2002). Similar patterns of entrainment have also been observed in biological systems (Strogatz & Stewart, 1993), and as such, biological synchrony may be relevant to the development of musicality on multiple levels. This includes synchronization between the brain and musical stimuli, synchronization of distinct brain regions within an individual, and synchronization between individuals within a group.

At the most basic level, music can be thought of as the highly ordered structuring of oscillatory pressure waves within a fluid medium. At the same time,
brains consist of neurons that fire in highly complex oscillatory patterns. As such, it follows that musical stimuli would be particularly well suited for the entrainment of neural activity. Not only has neural activity measured by EEG been shown to synchronize to musical beat in humans (Nozaradan, Zerouali, Peretz, & Mouraux, 2013), but this neural entrainment has even been observed in young infants (Cirelli, Spinelli, Nozaradan, & Trainor, 2016). This suggests an innate ability of the human brain to entrain to musical information, and may serve to explain and predict certain behavioral responses to music. For example, patients with Parkinson’s disease have been shown to improve in gait following music-based therapy (Pacchetti et al., 2000), possibly reflecting synchronization of motor systems with musical stimuli. Moreover, new technologies, such as brain.fm, are attempting to alter behavioral outcomes of neural entrainment to musical stimuli by modulating frequency bands known to be associated with focused and relaxed neural states (Buzsáki & Draguhn, 2004).

Not only have neural patterns been shown to entrain to musical stimuli, but musicality has also been associated with increased connectivity patterns between brain regions. This is not merely limited to connections within the auditory processing network, but also includes connections between auditory regions and other cognitive domains (Paraskevopoulos, Kraneburg, Herholz, Bamidis, & Pantev, 2015). For example, individual emotional responses to music can vary significantly (Mas-Herrero et al., 2014), and those that demonstrate a strong emotional response to music tend to show higher white matter connectivity between auditory and reward regions (Sachs et al., 2016). Conversely, white matter connectivity of these same regions has
been shown to be altered in an individual with music specific anhedonia, a condition in which one lacks a specific affective response to music (Loui et al., 2017). These white matter structural connections could be serving as a support system for the neural synchronization of these music and reward processing areas, and in fact we do see that individuals with musical anhedonia show decreased functional connectivity between right auditory cortex and nucleus accumbens during a musical reward task (Martínez-Molina et al., 2016).

Music can even serve as a conduit for increased synchronization between individuals within a group. Group dance and other such behavioral synchronization in response to music is often viewed as a natural extension of musicality, and work done by the McMaster LIVELab has shown that groups show increased head motion in a live music condition as compared to an album playback concert (Swarbrick et al., 2018). As of yet unpublished work by this same lab also suggest that neural synchrony of audience members, as measured by EEG, increases during live music performances (University of Western Ontario, 2018).

Effects of music on group cohesion are not limited to the duration of a musical performance either. In fact, studies of group dance (Mogan et al. 2017; Rennung & Göritz 2016) and group singing (Pearce et al., 2015) have shown that participation in such activities causes increased prosocial behavior and feelings of closeness, even when compared to other group activities. Neural synchronization may play a role in this effect, though it likely also driven by synchronized activation of the endogenous opioid system during group music making and dance, which in turn reinforces
prosocial behaviors (Tarr, Launay, & Dunbar, 2014). These social benefits of group music and dance could have proven particularly useful in early human societies, and as such group cohesion likely represents the earliest and most significant selective force for the development of musicality within the brain (Dunbar, 2012).

However, the goal of this paper is not to identify a single ultimate purpose for musicality. Instead, we suggest a strong association between musicality and neural synchrony to, of, and between brains, thus outlining a potential biological mechanism on which selection could impact the development of musicality systems within the brain. This is not to say that neural synchrony falls into the sole purview of musicality either. Many high order cognitive behaviors, such as creativity (Beaty et al., 2016; Beaty et al., 2018), have been associated with coactivation of many disparate brain regions, and comparisons of resting state functional connectivity related to musical and creative experience will be the topic of the next chapter. Neural synchrony may be a critical factor for high order cognition in general, but the complex oscillatory structure of music makes it particularly well suited for inducing neural synchrony, and a number of neural mechanisms that seem to promote music-associated neural synchrony suggests that evolution of this musical synchrony system has in fact occurred.

In summation, by the time that the earliest musical behaviors arose in humans, all the individual brain regions currently associated with the production and processing of musical information may have already been formed. Nonetheless, this is an insufficient basis for the claim that musicality is not an evolved system, as
selection could instead be acting on the intrinsic connections between these cognitive processing centers. In particular, neural entrainment to musical stimuli may have served as a physical basis for the increased synchronization between both individual brain regions and individual members of a group, and thus selective forces could then act on brain processes supporting these forms of neural synchrony. This represents a way in which we should be fundamentally shifting our view of the evolution of highly complex cognitive behaviors, of which musicality is only one example. More and more, we are seeing that high order cognition is not controlled by the actions of individual processing modules, but rather by the actions of broader cortical networks (Fox et al., 2005, Zabelina & Andrews-Hanna, 2016). There is no reason that a genetic predisposition towards connectivity of any number of brain regions wouldn’t exist, and as such, the evolutionary history of high order cognition is likely to be characterized by selection of new and stronger connections between independently functioning brain regions, which in turn produce novel and adaptive behaviors when working in synchrony.
Chapter 2. Differentiating Roles of Improvisational and Non-Improvisational Music Training in Resting State Functional Connectivity
Section 1. Introduction

Creativity is a complex and dynamic behavior, one that has challenged those within the cognitive fields for the better part of a century. Most commonly defined as “the ability to produce work that is both novel (i.e. original, unexpected) and appropriate (i.e. useful, adaptive concerning task constraints)” (Sternberg, 1999, p. 3), creativity researchers have long asked how people create such novel and appropriate works, what neural systems are recruited for such processing, and why individuals can differ so greatly in creative ability. In addressing the first of these questions within the creative domain of musical improvisation, Jeff Pressing proposed a behavioral model that suggested a balance between automatic retrieval of candidate musical sequences from long term memory and conscious appraisal of such sequences over the course of an improvisational performance (Pressing, 1988). This interplay of “generative” and “evaluative” behaviors has since become generalized to other domains of creativity, and is the basis of the “dual-process theory” of creative behavior (Sowden, Pringle, & Gabora, 2015).

Recent work by Roger Beaty and colleagues has identified the default mode network (DMN), executive control network (ECN), and salience network as three cortical hubs that may underlie the dual processes of creative cognition (Beaty, Benedek, Kaufman, & Silvia, 2015; Beaty et al., 2018). It has been suggested that the default mode network, which has been closely associated with self-referential processing and mental simulations (Kim & Johnson, 2014; Mitchell, Macrae, &
Banaji, 2006), underlies idea generation, whereas the more goal oriented executive control network (Fox et al., 2005; Zabelina & Andrews-Hanna, 2016) underlies idea evaluation (Beaty et al., 2015). While traditionally these two networks are thought of as highly anti-correlated (Fox et al., 2005, Zabelina & Andrews-Hanna, 2016), areas of the salience network have been observed to facilitate switching between default and executive processes (Sridharan, Levitan, & Menon, 2008; Uddin, 2015), and therefore may support the dynamic interplay between generative and evaluative processes during creative cognition (Beaty et al, 2018).

Returning to the behavioral model originally proposed by Jeff Pressing (1988), it would follow that the same networks thought to underlie generative and evaluative processes in domain general creative behavior would also play a role within the specific domain of musical improvisation. Previous work has already established a role of both DMN and ECN in musical improvisation, with DMN showing increased activity during lower constraint improvisation tasks (Limb & Braun, 2008; Liu et al., 2012), and ECN showing increased activity during higher constraint improvisation tasks (Bengtsson, Csíkszentmihályi, & Ullén, 2014; Pinho, de Manzano, Fransson, Eriksson, & Ullén, 2014). Previous work has already shown that differences in task constraints can account for these differences in ECN and DMN activity (Pinho, Ullén, Castelo-Branco, Fransson, & de Manzano, 2015). This is consistent with the dual process theory, as higher task constraints would relate to a higher relevance of evaluative processes, and therefore increased action of the ECN,
whereas lower constraint tasks could rely more on generative processing by the DMN.

Given the alignment of behavioral models of musical improvisation (Pressing, 1988), altered connectivity profiles associated with generalized creative behaviors (Beaty et al., 2015; Beaty et al., 2018), and task fMRI studies of musical improvisation (Limb & Braun 2008; Liu et al., 2012; Bengtsson et al., 2014; Pinho et al., 2014), we fully expect to see an altered role of ECN and DMN in a population of improvisational musicians. Here, we add to the existing body of literature in two ways. First, we sought to observe whether a population of improvisationally trained musicians showed altered functional connectivity patterns in the absence of task, as has been observed in populations of individuals exhibiting high domain general creativity as measured by divergent thinking tasks (Beaty et al., 2018; Takeuchi et al., 2012). Second, we sought to differentiate the role of improvisational music training and that of general music training in any differences in resting state functional connectivity that we observe.

Up to this point, only one major study has differentiated between improvisational and non-improvisational musical experience (Pinho et al., 2014). However, there are a number of studies indicating that the same networks we consider to be important to creative behaviors are also relevant to musical processing. Musical training has been associated with increased executive functioning (Moreno et al., 2011) and increased functional connectivity of the salience network (Luo et al., 2014). Moreover, default mode activity has been associated with a number of musical
behaviors, including aiding in the tracking of tonal stimuli (Janata et al., 2002), associating music with memories (Janata, 2009), and the aesthetic response to music (Williams, Johnson, Curtis, King, & Anderson, 2018). Considering this, it is possible that differences we observe in the functional connectivity profiles of improvisational musicians could be a result of general musical training rather than improvisational training in particular.

Here, we compare resting state functional networks within a sample of improvisational musicians to those of classical musicians and minimally musically trained (MMT) controls. We use these groups as a means of studying the impact of both presence and type (improvisational focused vs non-improvisational focused) of musical experience on resting state functional connectivity. We do this at both a global cortical level, and more locally at the level of specific resting state networks. We seek to distinguish between three competing hypotheses with these data. Differences in resting functional connectivity related to musical experience could be primarily associated with general music training, improvisational music training in particular, or instead the two forms of training have independent effects on connectivity profiles. We find the last of these hypotheses to be the most likely, and expect improvisational training in particular to be associated with connections between default mode, executive control, and salience networks, consistent with the tradeoff of generative and evaluative functions required for musical improvisation (Pressing, 1988) and the connectivity profiles thought to underlie such creative behaviors (Beaty et al, 2018).
Section 2. Methods

2.1 Subjects. Thirty-six subjects were recruited from Wesleyan University and the Hartt School of Music and received monetary compensation or course credit for their participation. Subjects were categorized into Improvisational, Classical, or Minimally Musically Trained (MMT) groups based on their reported musical experience. Worth noting is the fact that due to an inability to recruit a sufficient sample of female improvisational musicians, this study was limited to male participants.

The improvisational group (n = 12) was defined by the following criteria: 1) 5+ years of training in music that included improvisation, and 2) Current participation in improvisatory musical activities for 1+ hours per week. The improvisational musical experience of this group fell primarily within the jazz domain. The classical group (n = 12) was defined by the following criteria: 1) 5+ years of musical training, and 2) Current participation in non-improvisational musical activities for 1+ hour per week. The minimal musical training (MMT) group (n = 12) included participants who had less than 5 years of previous musical training.

The three groups were matched in age, general intelligence as measured by the Shipley abstraction test (Shipley, 1940), short term memory as measured by the digit span task (Baddelay, 2003), low-level pitch discrimination ability (Loui, Guenther, Mathys, & Schlaug, 2008), and age of onset of musical training (Table 1). Both the improvisational and classical groups had a longer duration of musical training than MMT, but there was no significant difference between the
improvisational and classical groups. The jazz group had an average of 5.4 years of training in musical improvisation, which was significantly higher than both the classical and MMT groups, who had 0.9 and 0 years of musical improvisation training respectively. Subjects from the jazz group reported improvisatory musical activities in one or more instruments including piano (n = 8), bass (2), guitar (3), mandolin (1), voice (1), drum (4), clarinet (1), saxophone (3), and vibraphone (1). Subjects from the classical group reported non-improvisatory musical activities in piano (n = 2), bass (2), guitar (4), drum (3), clarinet (2), baritone (1), violin (1), saxophone (1), french horn (1), and pipa (1). All subjects gave informed consent as approved by the Institutional Review Boards of Wesleyan University and Hartford Hospital.

<table>
<thead>
<tr>
<th></th>
<th>Minimally Musically Trained (MMT) (n=12 males)</th>
<th>Classical Musicians (n=12 males)</th>
<th>Improvisational Musicians (n=12 males)</th>
<th>All Subjects (n=36 males)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pitch Discrimination (Hz)</strong></td>
<td>7.8 (4.9)</td>
<td>4.1 (2.4)</td>
<td>4.1 (2.1)</td>
<td>5.1 (3.5)</td>
</tr>
<tr>
<td><strong>Digit Span (digits)</strong></td>
<td>7.5 (1.3)</td>
<td>8.1 (1.9)</td>
<td>7.9 (1.4)</td>
<td>7.9 (1.5)</td>
</tr>
<tr>
<td><strong>Shipley (raw score)</strong></td>
<td>17.7 (0.5)</td>
<td>17.9 (1.5)</td>
<td>17.3 (1.8)</td>
<td>17.7 (1.4)</td>
</tr>
<tr>
<td><strong>Age of onset (years)</strong></td>
<td>9.8 (2.3)</td>
<td>8.2 (3.4)</td>
<td>8.4 (2.5)</td>
<td>8.6 (2.8)</td>
</tr>
<tr>
<td><strong>Duration of training (years)</strong></td>
<td>0.9(1.4)</td>
<td>10.1 (3.7)</td>
<td>8.4 (3.2)</td>
<td>6.7 (4.9)</td>
</tr>
<tr>
<td><strong>Duration of improv training (years)</strong></td>
<td>0 (0)</td>
<td>0.9 (1.3)</td>
<td>5.4 (3.4)</td>
<td>2.3 (3.2)</td>
</tr>
</tbody>
</table>

*Table 1.* performance on baseline behavioral tasks by group. For each task, the first number represents the mean value for the group, and the parenthetical number represents the standard deviation.
2.2 Procedures. After subjects gave informed consent, they completed the baseline tasks for the experiment (see subjects section above). Subjects then completed a questionnaire on their musical background, including questions about the age of onset of musical training, the duration of general musical training, and the duration of jazz and improvisation training (Table 1). A partially overlapping sample of participants also performed a short version of the Torrance test of divergent thinking (Torrance, 1968) and a musical improvisation task (Zeng, Przysinda, Pfeifer, Arkin, & Loui, 2017). Previous work has shown that classical musicians from this sample perform higher than MMT controls on fluency measures of the divergent thinking task, whereas both musician groups performed better than controls on originality measures from the same task (Przysinda, Zeng, Maves, Arkin, & Loui, 2017). In the musical improvisation task, the Improvisational group was given significantly higher creativity ratings by expert jazz musicians (Zeng et al., 2017). However, the current sample includes participants from other studies that did not include these measures, so robust group comparisons of these behavioral measures was not possible.

2.2.1 MRI Acquisition. High-resolution T1 and resting state images were acquired in a 3T Siemens Skyra MRI scanner at the Olin Neuropsychiatry Research Center at the Institute of Living. The anatomical images were acquired using a T1-weighted, 3D, magnetization-prepared, rapid-acquisition, gradient echo (MPRAGE) volume acquisition with a voxel resolution of 0.8 x 0.8 x 0.8 mm³. Resting state MRI was
acquired as 947 contiguous echo planar imaging (EPI) functional volumes (TR = 475 ms; TE = 30 ms; flip angle = 90, 48 slices, matrix = 80 x 80; FOV = 240 mm; acquisition voxel size = 3 x 3 x 3 mm³). Subjects kept their eyes open and fixated on a cross on the screen during resting state data acquisition.

2.2.2 MRI Preprocessing. Resting state preprocessing was carried out using the CONN Toolbox default preprocessing pipeline (Whitfield-Gabrieli & Nieto-Castanon, 2012). In order, this consisted of functional realignment and unwarp, functional center to origin, functional slice timing correction, functional outlier detection, functional direct segmentation and normalization, structural center to origin, structural segmentation and normalization, and functional smoothing using an 8mm smoothing kernel. Denoising steps included correction for confounding effects of white matter, cerebrospinal fluid, realignment parameters, scrubbing, and the effect of rest, band pass filtering to a range of 0.008-0.09, and linear detrending.

2.2.3 Seed to Voxel Analysis. We selected the medial prefrontal cortex and lateral prefrontal cortex, as defined by the CONN Toolbox networks atlas (Whitfield-Gabrieli & Nieto-Castanon, 2012), as a priori seed regions, due to their significance as primary default mode and executive control regions respectively (Fox et al., 2005; Zabelina & Andrews-Hanna, 2016). We then identified additional seed regions from within the default mode, executive control, and salience networks that contained connectivity clusters showing a significant main effect of group. For each such
region, group seed-based connectivity profiles were compared, and significant clusters from individual group contrasts were extracted (Appendix A). Locations for these clusters are defined using the CONN structural atlas (Whitfield-Gabrieli & Nieto-Castanon, 2012).

2.2.4 Voxel to Voxel Analysis. Group independent component analysis (ICA) was performed through CONN Toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012) in order to separate the cortex into 20 functionally distinct components with a dimensionality reduction variable of 64. These 20 components were then matched to templates of known functional networks, and the component most closely resembling the default mode network was identified. This component was then used as the basis for group level comparisons, as well as contrasts between the duration of improvisational music training and the duration of general music training.

2.2.5 ROI to ROI Analysis. Correlation matrices comparing all 32 regions of the CONN networks atlas (Whitfield-Gabrieli & Nieto-Castanon, 2012) were extracted for each participant. These Matrices were then exported into MATLAB and analyzed using the Brain Connectivity Toolbox (Rubinov & Sporns, 2010). Component sizes for averaged group connectivity matrices were calculated across a range of threshold values in order to determine an appropriate proportional threshold for subsequent analyses. Louvain community detection was then performed for each averaged group connectivity matrix, and modularity statistics created by Louvain community
detection of individual correlation matrices were compared across groups. Global level comparisons of degrees, clustering coefficients, strengths, betweenness centrality, and local efficiency were then performed. Finally, individual node comparisons for each of these measures were performed for the four DMN nodes, four ECN nodes, and seven salience network nodes. This last round of analyses was then corrected for multiple comparisons using the Benjamini-Hochberg (1995) procedure as accessed by the Handbook of Biological Statistics (McDonald, 2014).

Section 3. Results

3.1 Seed-Based Connectivity Analysis. Significant clusters demonstrating a main effect of group were observed for one of four DMN seeds, the posterior cingulate cortex (PCC), as well as the left lateral prefrontal cortex (lLPFC), Left Posterior Parietal Cortex (lPPC), and right posterior parietal cortex (rPPC) from the ECN (p < 0.05, p-FDR corrected, Appendix A). However, no salience areas demonstrated any such significant clusters. Therefore, we limit our analysis of seed-based connectivity profiles and individual group contrasts to the mPFC (Figure 1A), the PCC (Figure 3A), and the three significant ECN seed regions (Figure 5A, Figure 7A, Figure 8A).

3.1.1 Medial Prefrontal Cortex. Group mPFC connectivity profiles (Figure 1B) were consistent with classically observed patterns of DMN connectivity (Fox et al., 2005). Both musician groups tended to show broader mPFC connectivity profiles than MMT
Figure 1. Medial Prefrontal Cortex Connectivity Profiles by Group. A: mPFC seed region (radiological view). B: Anatomical view of individual group mPFC connectivity profiles after $p < 0.001$ p-FDR height threshold correction and $p < 0.05$ peak-voxel p-FWE correction.
controls, notably including connectivity to DMN areas and parts of ventrolateral and medial temporal lobe (Figure 1B). One significant cluster spanning the inferior portion of the lateral occipital cortex and the temporal occipital fusiform cortex was observed in an Improvisational > MMT group contrast, and two significant clusters including portions of the precuneus cortex and left inferior frontal gyrus were observed in a Classical > MMT group contrast (Figure 2, Appendix A).

**Figure 2. Medial Prefrontal Cortex Seeded Group Contrasts.** Significant clusters for mPFC seeded Improvisational > MMT (top) and Classical > MMT (bottom) group contrasts.
Figure 3. Posterior Cingulate Cortex Connectivity Profiles by Group. A: PCC seed region (radiological view). B: Anatomical view of individual group PCC connectivity profiles after $p < 0.001$ p-FDR height threshold correction and $p < 0.05$ peak-voxel p-FWE correction.
3.1.2 Posterior Cingulate Cortex. group PCC connectivity profiles differed slightly from classical patterns of DMN connectivity (Fox et al., 2005), especially in that classical musicians did not show highly significant PCC seeded connectivity to mPFC (Figure 3B). However, similar to the mPFC seed, increased connectivity patterns were observed between PCC and ventral temporal areas, this time bearing significant clusters in both Improvisational > MMT and Classical > MMT group contrasts (Figure 4, Appendix A). Additional significant PCC seeded Classical > MMT clusters were observed in portions of the right cerebellum and left frontal pole (Figure 4, Appendix A).

Figure 4. Posterior Cingulate Cortex Seeded Group Contrasts. Significant clusters for PCC seeded Improvisational > MMT (top) and Classical > MMT (bottom) group contrasts.
Figure 5. Left Lateral Prefrontal Cortex Connectivity Profiles by Group. A: lLPFC seed region (radiological view). B: Anatomical view of individual group lLPFC connectivity profiles after p < 0.001 p-FDR height threshold correction and p < 0.05 peak-voxel p-FWE correction.
3.1.3 Left Lateral Prefrontal Cortex. ILPFC group connectivity profiles (Figure 5B) demonstrated the traditional ECN pattern of lateral prefrontal and lateral parietal connectivity (Fox et al., 2005). In addition, both musician groups displayed connectivity patterns between ILPFC and caudolateral temporal lobe areas not seen in MMT controls. This was colocalized with a significant cluster in the Improvisational > MMT contrast, in addition to a significant cluster spanning the left lingual gyrus, right cuneal cortex, and right occipital pole (Figure 6, Appendix A). Furthermore, the Improvisational > Classical group contrast included five significant clusters spanning portions of bilateral insular cortex, left central opercular cortex, bilateral postcentral gyrus, and bilateral superior parietal lobule (Figure 6, Appendix A).

![Figure 6. Left Lateral Prefrontal Cortex Seeded Group Contrasts.](image)

*Figure 6. Left Lateral Prefrontal Cortex Seeded Group Contrasts.* Significant clusters for ILPFC seeded Improvisational > MMT (top) and Improvisational > Classical (bottom) group contrasts.
Figure 7. Left Posterior Parietal Cortex Connectivity Profiles by Group. A: lPPC seed region (radiological view). B: Anatomical view of individual group lPPC connectivity profiles after p < 0.001 p-FDR height threshold correction and p < 0.05 peak-voxel p-FWE correction.
Figure 8. Right Posterior Parietal Cortex Connectivity Profiles by Group. A: rPPC seed region (radiological view). B: Anatomical view of individual group rPPC connectivity profiles after p < 0.001 p-FDR height threshold correction and p < 0.05 peak-voxel p-FWE correction.
3.1.4 Posterior Parietal Cortex. Group connectivity profiles for right PPC (Figure 7B) and left PPC (Figure 8B) were similar to one another and shared with other seed regions in trending towards larger connectivity clusters in the two musician groups as compared to MMT controls. For both lPPC and rPPC, only one significant cluster was observed within the Improvisational > MMT group contrast (Figure 9, Appendix A). However, this cluster was quite large, in both cases spanning portions of bilateral lingual gyrus, bilateral intracalcarine cortex, bilateral cuneal cortex, and left lateral occipital cortex (Figure 9, Appendix A).

Figure 9. Posterior Parietal Cortex Seeded Group Contrasts. Significant clusters for Improvisational > MMT group contrasts in lPPC (top) and rPPC (bottom) seeded analysis.
3.2 Independent Component Analysis. Our DMN component was primarily characterized by strong role of the PCC paired with anticorrelations to lateral prefrontal cortices (Figure 10A). While these patterns are consistent with DMN (Fox et al., 2005; Zabelina & Andrews-Hanna, 2016), this component notably lacks a strong role of the medial prefrontal cortex (Figure 10A). Whatever small ventromedial frontal clusters do exist across the entire sample completely disappear when observing individual group profiles for this component (Figure 10). Otherwise, the group component profiles established a similar pattern of DMN connectivity to that of the entire sample, although there was one area of superior frontal negativity present in the Classical and MMT groups that was not present in the Improvisational musicians (Figure 10B).

Group comparisons for our DMN component produced one significant cluster in the Improvisational > Classical contrast (Figure 11, Appendix A). In order to better disentangle effects of improvisational and non-improvisational music training, we also performed contrasts between duration of improvisational music training (ImprovMusTrain) and duration of general musical training (GenMusTrain) for our DMN component. The ImprovMusTrain > GenMusTrain contrast produced two significant clusters, one with a similar localization as the Improvisational > Classical group contrast, and the other including a portion of the left inferior frontal gyrus (Figure 11). One significant cluster was identified in the GenMusTrain > ImprovMusTrain, this time located within a portion of the right supramarginal gyrus (Figure 11).
Figure 10. Default Mode Network Component. ICA identified component most closely resembling DMN visualized across the entire sample (A) and for individual groups (B) after $p < 0.001$ p-FDR height threshold correction and $p < 0.05$ peak-voxel p-FWE correction.
Figure 11. Default Mode Network Component Contrasts. Significant clusters for Improvisational > Classical (top), ImprovMusTrain > GenMusTrain (middle), and GenMusTrain > ImprovMusTrain (bottom) contrasts within ICA identified DMN component.
3.3 Graph Theory Analysis. Analysis of maximum component sizes using the get component function of the brain connectivity toolbox (Rubinov & Sporns, 2010) indicated that all 32 Roi’s form a cohesive network starting at a proportional threshold of 0.2 (Figure 12A). As such, we used this threshold value for all subsequent analyses.

3.3.1 Louvain Community Detection. Significant group differences were observed in modularity as measured by Louvain community detection (Rubinov & Sporns, 2010). Modularity at a gamma threshold of one for individual connectivity matrices demonstrated a significant main effect of group (One way ANOVA, p < 0.05), and modularity of group averaged connectivity matrices provided evidence that these group differences persist across a spectrum of gamma thresholds (Figure 12 B, C). At a gamma threshold of one, a typical improvisational and MMT group averaged Louvain community assignment segregated the 32-node network atlas (Whitfield-Gabrieli & Nieto-Castanon, 2012) into five distinct communities, whereas the classical group was segregated into only three communities (Figure 13, Table 2). While the structuring of these communities was similar across groups, Improvisational musicians demonstrated a strong connection between DMN and visual regions not seen in the other two groups, as well as segregation of the salience and language networks into their own separate communities (Figure 13, Table 2).
Figure 12. Group Differences in Network Modularity. A: component sizes by matrix threshold for group averaged connectivity matrices. B: Louvain modularity statistic for group averaged connectivity matrices as a function of gamma. C: significant group comparison of individual Louvain modularity statistics at gamma = 1 (One-way ANOVA, p < 0.05) driven by differences between Improvisational and Classical musicians (Tukey HSD p = 0.022)
<table>
<thead>
<tr>
<th>Network</th>
<th>Region</th>
<th>Improvisational</th>
<th>Classical</th>
<th>MMT</th>
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<td></td>
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<tr>
<td></td>
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<td>LP (R) [47, -67, 29]</td>
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<td></td>
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<tr>
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<tr>
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<td>Anterior Insula (R) [47, 14, 0]</td>
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<td>SMG (R) [62, -35, 32]</td>
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<tr>
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<td>IPS (R) [39, -42, 54]</td>
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<tr>
<td></td>
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<td>pSTG (R) [-59, -42, 13]</td>
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<tr>
<td></td>
<td>Posterior (R, 79, -32)</td>
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*Table 2. Representative Louvain Community Assignments by Network.* 32 network nodes were segregated into communities for Improvisational, Classical, and MMT group averaged connectivity matrices.
Figure 13, Visualization of Representative Louvain Community Assignments. For improvisational and MMT groups, community 1 = yellow, community 2 = dark blue, community 3 = light blue, community 4 = orange, and community 5 = green. For classical group, community 1 = dark blue, community 2 = light blue, and community 3 = orange. See Table 2 for a breakdown of nodes by network and community assignment for each group.
3.3.2 *Global and Individual Node Small World Brain Connectivity*. Network measures of degree, the number of nodes significantly correlated to a node, strength, the sum of the correlation coefficients for a given node, clustering coefficient, the fraction of nodes correlated with a given node that are also correlated with one another, and local efficiency, the average connectedness in the neighborhood of a given node, did not show a significant main effect of group when examined across all 32 nodes of our atlas. However, there was a significant main effect of group on betweenness centrality (One-way ANOVA, p < 0.05), the number of shortest paths from one node to another that contains a given node (Figure 14A), primarily driven by differences between Classical and MMT groups (Tukey HSD, p = 0.017). For individual node comparisons of these same measures, only clustering coefficient and local efficiency of lPPC showed a marginal effect of group (Benjamini-Hochberg p = 0.083) once correcting for multiple comparisons (Figure 14B, C).
Figure 14 Global and Local Group Differences in Small World Connectivity. A: Individual measures of betweenness centrality averaged across group and presented as an average across all 32 nodes by group (One-way ANOVA, p = 0.0158). This effect was primarily driven by differences between Classical and MMT groups (Tukey HSD p = 0.017). B-C: group averages of local efficiency (B) and clustering coefficient (C) for left posterior parietal cortex (One way ANOVA, Benjamini-Hochberg p = 0.083). These effects were primarily driven by differences between Improvisational group and the other two groups (Tukey HSD, p < 0.05).
Section 4. Discussion

4.1 Differences in Resting State Connectivity Related to General Music Training.

Seed based group connectivity profiles for ECN and DMN regions showed a uniform trend towards more and larger highly significant connectivity clusters in both musician groups as compared to MMT controls. We did not, however, see any of the musical training related increases in salience network functional connectivity that has been previously reported (Luo et al., 2014). Where connectivity differences related to general musical training did exist, they tended to be in one of two forms. The first were differences in intrinsic network connectivity. That is, group profiles of DMN seeds tended to show more connectivity to other DMN regions, and ECN seeds tended to show more connectivity to other ECN regions within the musician groups. These differences did not bear any significant clusters with ECN seeded group contrasts, but Classical > MMT contrasts did identify clusters of increased connectivity between PCC and a portion of the mPFC, as well as between mPFC and a portion of the precuneus cortex, another default mode associated area (Fransson & Marrelec, 2008). Previous findings have associated music training with precuneus connectivity to other networks in a sample of female college students, but this effect did not extend to intrinsic DMN connectivity (Tanaka & Kirino, 2016). Therefore, we provide early evidence for a role of musical training in producing a more intrinsically connected DMN, as well as providing limited support to previous work indicating a role of musical training in increasing executive function (Moreno et al, 2011).
The second set of findings related to general musical training were in regards to DMN and ECN connectivity with other regions commonly associated with music processing. Classical > MMT contrasts demonstrated increased connectivity between mPFC and left inferior frontal gyrus (LIFG). While primarily considered a language processing area, LIFG has also been associated with domain-general auditory tasks (Müller & Basho, 2004) and musical syntax processing (Maess, Koelsch, Gunter, & Friederici, 2001). LIFG has also been shown to adapt structurally to musical training. Orchestral musicians have denser LIFG (Sluming et al., 2012), white matter from LIFG is larger in singers (Halwanie et al., 2011), and there is even causal evidence demonstrating that auditory-motor training in a musical task increases white matter connectivity to LIFG (Moore, Schaefer, Bastin, Roberts, & Overy, 2017; Halwani, Loui, Rueber, & Schlaug, 2011). In addition to LIFG, ICA indicated a primary role of general music training, rather than improvisational music training, in explaining connectivity between DMN and right supramarginal gyrus. This is consistent with the known role of the supramarginal gyrus in pitch memory (Vines, Schnider, & Schlaug, 2006), as retrieval of pitch information is likely to be relevant to improvisational and non-improvisational musicians alike.

Moreover, possibly the most intriguing result within this second set of findings relates to differences in DMN and ECN connectivity to primary auditory cortex. Both mPFC and PCC showed higher connectivity with ventral temporal areas than was observed in MMT controls, showing significant clusters in Improvisational > MMT and Classical > MMT group contrasts in the case of PCC. On the other hand,
both musician groups showed higher LLPFC seeded connectivity than MMT controls with dorsal temporal areas, this time demonstrating significant clusters in the Improvisational > MMT group contrast. This suggests that DMN regions may be more preferentially coactivating with ventrolateral “what” auditory pathways in musicians, whereas the ECN associated lateral prefrontal cortices of musicians may be more intrinsically connected to more caudolateral “where” pathways (Rauschecker & Tian, 2000; Arnott, Binns, Grady, & Alain, 2004). This is consistent with magnetoencephalography work suggesting musicians’ have more highly connected auditory cortices (Paraskevopoulos, Kraneburg, Herholz, Bamidis, & Pantev, 2015), but this is the first time musical training associated differences between DMN and ECN connectivity to Auditory processing pathways has ever been suggested.

4.2 Differences in Resting State Connectivity Related to Improvisation Specific Music Training. While many of the seed-based connectivity results reflected an association between DMN and ECN connectivity and general music training, two striking results seemed to be specific to improvisational training. First of these is the cluster of bilateral insular cortex from the LLPFC seeded Improvisational > Classical group contrast. Insular Cortex is an area closely associated with salience processing (Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004). This is in keeping with our hypothesis that improvisational music training, moreso than general music training, would be associated with increased connectivity among a group of networks composed in part by ECN and salience regions, which are thought to underlie the
evaluative and generative processes of highly creative behaviors (Beaty et al, 2015; Beaty et al., 2018).

We also noted a number of significant Improvisational > MMT group contrasts between ECN seed regions, as well as the PCC seed from DMN, and a broad cluster of occipital areas including bilateral lingual gyrus, bilateral intracalcarine cortex, bilateral cuneal cortex, and left lateral occipital cortex. This was not observed in Classical > MMT group contrasts, consistent with an emerging body of work done in EEG, DTI, and VBM methodological paradigms associating occipital lobe connectivity with domain general creativity (Petsche, 1996; Takeuchi et al., 2010; Fink et al., 2014). While not a part of the high creative network identified by Roger Beaty and Colleagues (2018), this agreement across a breadth of methodological approaches leads us to the conclusion that highly connected visual cortices, possibly serving a role in creative imagery, underlies domain general creativity.

Moving away now from Seed based connectivity results, ICA did lend some support to the hypothesis that there would be increased connectivity between DMN and ECN associated with improvisational specific music training. One cluster located in the right dorsolateral prefrontal cortex, an ECN associated region (Fox et al., 2005), was found to be significant in our Improvisational > Classical DMN component contrast. Not only this, but a similar cluster was found in our ImprovMusTrain > GenMusTrain contrast, providing the most direct evidence that it is the effect of improvisational music training rather than general musical training that
leads intrinsic functional connectivity differences between areas closely associated with creative behaviors (Beaty et al., 2015, Beaty et al., 2018). This same contrast also produced a significant cluster between the DMN component and part of the LIFG, in contrast to the previous finding that mPFC seeded connectivity to LIFG seemed more closely associated with general music training. Worth noting here is the fact that our DMN component lacked a significant contribution of mPFC, so one explanation of this difference is that while mPFC connectivity to LIFG may be more highly associated with general music training, connectivity between LIFG and other DMN components may be better explained by improvisation specific musical training.

Where group differences in small world brain connectivity did exist, they tended to be driven by differences between Improvisational and Classical musician groups. In the case of modularity, mean values for improvisational and classical groups were on opposite sides of MMT controls, with improvisational musicians showing significantly less modularity than classical musicians. Classical musicians also showed higher betweenness centrality than MMT controls across all nodes of our atlas, and improvisational musicians showed a trend towards lower clustering coefficient and local efficiency within the LPPC. This points towards a pattern of more diffuse connectivity in improvisational musicians at a global level, potentially contrasting with a preference for fewer, more tightly knit communities associated with non-improvisational music training.
4.3 Limitations and Future Directions. While these findings are fairly consistent with our hypotheses and the existing body of literature, there are certain limitations to our sample and experimental procedures that should be addressed. Previous work has pointed out that despite a lack of differences in standardized tests of creativity, women are less likely to assort into “highly creative” fields such as musical improvisation, likely due to sociocultural reasons (Baer & Kaufman, 2008). Within our sampling pool, we were unable to recruit any female improvisational musicians, and previous work indicating an impact of gender on functional connectivity (Schmithorst & Holland, 2006; Biswal et al., 2010; Zuo et al., 2010) and structural connectivity related to creativity (Ryman et al., 2014) led us to exclude female participants from Classical and MMT groups in order to avoid a gender confound within our sample. This meant we had to use data from male participants in other projects to fill out our Classical and MMT groups, rendering us without the alternative uses task and improvisation continuation task data needed to assess the role of creative performance on functional connectivity.

In the future, we will be recruiting and collecting behavioral task data from a much larger sample of both male and female participants, as well as continuing work comparing Improvisational, Classical, and MMT groups in terms of white matter connectivity (Zeng et al., 2017). We would also like to better determine causality in the association between different forms of musical training and brain connectivity. We would accomplish this by performing a longitudinal study on participants over the course of their musical training, and by comparing these intermediate level musicians
to those at both expert and novice levels. Finally, we would also be interested in exploring the impact of other modes of musical creativity on brain connectivity. In particular, musical composition has the same end result of a novel and appropriate musical product, but achieves this on a much slower time scale than musical improvisation. This may result in a greater role of evaluative processes, as well as a lesser role in dynamic interplay between generative and evaluative processes. Therefore, comparisons of improvisational and compositional musicianship may prove useful in better characterizing the neural networks underlying musical creativity.

4.4 Conclusions. Despite limitations in our sample, we were able to observe distinct roles of intermediate level improvisational and non-improvisational musical training in functional connectivity, even in the absence of task. These altered resting-state connectivity patterns can be explained in one of two ways. Either creative and musical individuals are more likely to be engaging in creative and musical thought processes at rest, or else these individuals have altered intrinsic connectivity patterns that represents a priming for creative and musical behaviors. Either way, these data provide evidence that musicality and creativity can be thought of as a distinct mental trait, rather than simply being a processing state.

In particular, the brains of improvisational musicians demonstrate more diffuse global resting state connectivity as measured by Louvain modularity (Rubinov & Sporns, 2010), with a prominent role of ECN, DMN, Salience, and Visual network
connectivity. This is consistent with previous literature suggesting these regions are critical for the dynamic interplay of generative and evaluative processes (Beaty et al., 2015; Beaty et al., 2018; Petsche, 1996) and imagery associated with creative ideation (Takeuchi et al., 2010; Fink et al., 2014). In contrast, general musical training was characterized by increased within network resting state connectivity of the DMN, and to a lesser extent the ECN. General music training was also associated with connectivity between these networks and auditory processing areas, with DMN showing a preference for connectivity to ventral auditory pathway, and ECN showing a preference for caudolateral auditory pathway.
Appendix A: Significant Clusters for Group

Comparisons

*Medial Prefrontal Cortex Seeded Connectivity:*

Improvisational > MMT:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
<th>peak p-FWE</th>
<th>peak p-unc</th>
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<tbody>
<tr>
<td>-48 -86 -08</td>
<td>368</td>
<td>0.007292</td>
<td>0.021941</td>
<td>0.000645</td>
<td>0.672448</td>
<td>0.000039</td>
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</tbody>
</table>

Cluster Atlas Locations:
- 163 voxels covering 8% of atlas.iLOC l (Lateral Occipital Cortex, inferior division Left)
- 72 voxels covering 11% of atlas.TOFusC l (Temporal Occipital Fusiform Cortex Left)
- 26 voxels covering 2% of atlas.LG l (Lingual Gyrus Left)
- 10 voxels covering 1% of atlas.OFusG l (Occipital Fusiform Gyrus Left)
- 1 voxel covering 0% of atlas.pTFusC l (Temporal Fusiform Cortex, posterior division Left)
- 96 voxels covering 0% of atlas.not-labeled

Classical > MMT:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
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<td>0.000060</td>
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Cluster Atlas Locations:
- 319 voxels covering 6% of atlas.Precuneous (Precuneous Cortex)
- 143 voxels covering 2% of atlas.FP l (Frontal Pole Left)
- 117 voxels covering 7% of atlas.FOrb l (Frontal Orbital Cortex Left)
- 81 voxels covering 12% of atlas.IFG tri l (Inferior Frontal Gyrus, pars triangularis Left)
- 24 voxels covering 33% of atlas.SCC l (Supracleareine Cortex Left)
- 6 voxels covering 1% of atlas.ICC l (Intracleareine Cortex Left)
- 5 voxels covering 1% of atlas.Cuneal l (Cuneal Cortex Left)
- 5 voxels covering 0% of atlas.LG l (Lingual Gyrus Left)
- 1 voxel covering 0% of atlas.PC (Cingulate Gyrus, posterior division)
- 1 voxel covering 0% of atlas.FO l (Frontal Operculum Cortex Left)
- 248 voxels covering 0% of atlas.not-labeled

*Posterior Cingulate Cortex Seeded Connectivity:*

Main Effect of Group:

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<th>size p-FDR</th>
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Cluster Atlas Locations:
- 290 voxels covering 12% of atlas.TP l (Temporal Pole Left)
227 voxels covering 3% of atlas.FP l (Frontal Pole Left)
46 voxels covering 2% of atlas.SFG l (Superior Frontal Gyrus Left)
36 voxels covering 2% of atlas.FOrb l (Frontal Orbital Cortex Left)
12 voxels covering 0% of atlas.FP r (Frontal Pole Right)
77 voxels covering 0% of atlas.not-labeled

Improvisational > MMT:
Clusters (x,y,z) size p-FWE size p-FDR size p-unc peak p-FWE peak p-unc
+46 +08 -46 373 0.005716 0.019410 0.000485 0.684558 0.000039
-38 +12 -46 293 0.017665 0.030174 0.001509 0.650708 0.000034
Cluster Atlas Locations:
274 voxels covering 12% of atlas.TP l (Temporal Pole Left)
202 voxels covering 8% of atlas.TP r (Temporal Pole Right)
108 voxels covering 33% of atlas.aITG r (Inferior Temporal Gyrus, anterior division Right)
3 voxels covering 1% of atlas.aTFusC r (Temporal Fusiform Cortex, anterior division Right)
79 voxels covering 0% of atlas.not-labeled

Classical > MMT:
Clusters (x,y,z) size p-FWE size p-FDR size p-unc peak p-FWE peak p-unc
-06 +60 +30 866 0.000029 0.000121 0.000003 0.120438 0.000002
+06 -52 -40 649 0.000278 0.000572 0.000025 0.346527 0.000011
-44 +08 -28 553 0.000812 0.001116 0.000073 0.478676 0.000020
Cluster Atlas Locations:
428 voxels covering 6% of atlas.FP l (Frontal Pole Left)
358 voxels covering 15% of atlas.TP l (Temporal Pole Left)
254 voxels covering 10% of atlas.Cereb1 r (Cerebelum Crus1 Right)
163 voxels covering 2% of atlas.FP r (Frontal Pole Right)
157 voxels covering 7% of atlas.Cereb2 r (Cerebelum Crus2 Right)
126 voxels covering 16% of atlas.Cereb9 r (Cerebelum 9 Right)
97 voxels covering 3% of atlas.SFG l (Superior Frontal Gyrus Left)
93 voxels covering 6% of atlas.FOrb l (Frontal Orbital Cortex Left)
36 voxels covering 8% of atlas.aMTG l (Middle Temporal Gyrus, anterior division Left)
31 voxels covering 1% of atlas.SFG r (Superior Frontal Gyrus Right)
29 voxels covering 17% of atlas.Ver9 (Vermis 9)
24 voxels covering 1% of atlas.Cereb8 r (Cerebelum 8 Right)
15 voxels covering 2% of atlas.Cereb9 l (Cerebelum 9 Left)
12 voxels covering 1% of atlas.Cereb6 r (Cerebelum 6 Right)
5 voxels covering 0% of atlas.PaCiG l (Paracingulate Gyrus Left)
1 voxels covering 0% of atlas.Cereb7 r (Cerebelum 7b Right)
1 voxels covering 1% of atlas.Ver10 (Vermis 10)
238 voxels covering 0% of atlas.not-labeled

Left Lateral Prefrontal Cortex Seeded Connectivity:

Main Effect of Group:
Clusters (x,y,z) size p-FWE size p-FDR size p-unc peak p-FWE peak p-unc
+06 -90 +14 533 0.000157 0.000014 0.000010 0.654678 0.000031
-14 -66 +00 239 0.017939 0.029651 0.001210 0.601771 0.000026

49
Cluster Atlas Locations:
- 148 voxels covering 11% of atlas.IC l (Insular Cortex Left)
- 131 voxels covering 9% of atlas.LG l (Lingual Gyrus Left)
- 127 voxels covering 20% of atlas.Cuneal r (Cuneal Cortex Right)
- 109 voxels covering 7% of atlas.SPL l (Superior Parietal Lobule Left)
- 94 voxels covering 4% of atlas.OP r (Occipital Pole Right)
- 83 voxels covering 13% of atlas.ICC l (Intralcalcarine Cortex Left)
- 51 voxels covering 1% of atlas.PostCG l (Postcentral Gyrus Left)
- 38 voxels covering 2% of atlas.LG r (Lingual Gyrus Right)
- 35 voxels covering 7% of atlas.Cuneal l (Cuneal Cortex Left)
- 34 voxels covering 24% of atlas.SCC r (Supracalcarine Cortex Right)
- 22 voxels covering 30% of atlas.SCC l (Supracalcarine Cortex Left)
- 18 voxels covering 2% of atlas.CO l (Central Opercular Cortex Left)
- 10 voxels covering 1% of atlas.ICC r (Intracalcarine Cortex Right)
- 9 voxels covering 0% of atlas.OP l (Occipital Pole Left)
- 8 voxels covering 2% of atlas.FO l (Frontal Operculum Cortex Left)
- 6 voxels covering 1% of atlas.Putamen l
- 517 voxels covering 0% of atlas.not-labeled

Improvisational > MMT:
Clusters (x,y,z) size p-FWE size p-FDR size p-unc peak p-FWE peak p-unc
+06 -96 +14 1983 0.000000 0.000000 0.000000 0.114800 0.000002
-60 -52 -12 573 0.000590 0.001275 0.000052 0.631355 0.000034

Cluster Atlas Locations:
- 337 voxels covering 39% of atlas.toMTG l (Middle Temporal Gyrus, temporooccipital part Left)
- 261 voxels covering 41% of atlas.Cuneal r (Cuneal Cortex Right)
- 258 voxels covering 10% of atlas.OP r (Occipital Pole Right)
- 255 voxels covering 17% of atlas.LG l (Lingual Gyrus Left)
- 185 voxels covering 29% of atlas.ICC l (Intracalcarine Cortex Left)
- 167 voxels covering 10% of atlas.LG r (Lingual Gyrus Right)
- 122 voxels covering 24% of atlas.Cuneal l (Cuneal Cortex Left)
- 98 voxels covering 2% of atlas.sLOC l (Lateral Occipital Cortex, superior division Left)
- 86 voxels covering 12% of atlas.toITG l (Inferior Temporal Gyrus, temporooccipital part Left)
- 63 voxels covering 44% of atlas.SCC r (Supracalcarine Cortex Right)
- 50 voxels covering 2% of atlas.iLOC l (Lateral Occipital Cortex, inferior division Left)
- 44 voxels covering 6% of atlas.ICC r (Intracalcarine Cortex Right)
- 39 voxels covering 1% of atlas.OP l (Occipital Pole Left)
- 28 voxels covering 0% of atlas.Precuneous (Precuneous Cortex)
- 24 voxels covering 33% of atlas.SCC l (Supracalcarine Cortex Left)
- 16 voxels covering 2% of atlas.TO FusC l (Temporal Occipital Fusiform Cortex Left)
- 3 voxels covering 1% of atlas.Ver6 (Vermis 6)
- 2 voxels covering 0% of atlas.sLOC r (Lateral Occipital Cortex, superior division Right)
- 1 voxels covering 0% of atlas.OFusG l (Occipital Fusiform Gyrus Left)
- 517 voxels covering 0% of atlas.not-labeled
### Improvisational > Classical:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
<th>peak p-FWE</th>
<th>peak p-unc</th>
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Cluster Atlas Locations:
- 716 voxels covering 20% of atlas.PostCG l (Postcentral Gyrus Left)
- 330 voxels covering 25% of atlas.IC r (Insular Cortex Right)
- 328 voxels covering 25% of atlas.IC l (Insular Cortex Left)
- 248 voxels covering 17% of atlas.SPL l (Superior Parietal Lobule Left)
- 220 voxels covering 7% of atlas.PostCG r (Postcentral Gyrus Right)
- 114 voxels covering 12% of atlas.CO l (Central Opercular Cortex Left)
- 98 voxels covering 2% of atlas.PreCG l (Precentral Gyrus Left)
- 94 voxels covering 6% of atlas.SPL r (Superior Parietal Lobule Right)
- 53 voxels covering 2% of atlas.TP r (Temporal Pole Right)
- 41 voxels covering 5% of atlas.Putamen l
- 38 voxels covering 4% of atlas.CO r (Central Opercular Cortex Right)
- 27 voxels covering 1% of atlas.TP l (Temporal Pole Left)
- 24 voxels covering 0% of atlas.Precuneous (Precuneous Cortex)
- 13 voxels covering 4% of atlas.FO l (Frontal Operculum Cortex Left)
- 8 voxels covering 0% of atlas.sLOC r (Lateral Occipital Cortex, superior division Right)
- 7 voxels covering 2% of atlas.FO r (Frontal Operculum Cortex Right)
- 6 voxels covering 2% of atlas.Pallidum l
- 4 voxels covering 0% of atlas.FOrb r (Frontal Orbital Cortex Right)
- 3 voxels covering 0% of atlas.aSMG l (Supramarginal Gyrus, anterior division Left)
- 3 voxels covering 1% of atlas.PP r (Planum Polare Right)
- 395 voxels covering 0% of atlas.not-labeled

### Left Posterior Parietal Cortex Seeded Connectivity:

Main Effect of Group:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
<th>peak p-FWE</th>
<th>peak p-unc</th>
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Cluster Atlas Locations:
- 547 voxels covering 32% of atlas.LG r (Lingual Gyrus Right)
- 469 voxels covering 31% of atlas.LG l (Lingual Gyrus Left)
- 399 voxels covering 62% of atlas.ICC l (Intracalcarine Cortex Left)
- 356 voxels covering 7% of atlas.sLOC l (Lateral Occipital Cortex, superior division Left)
- 328 voxels covering 44% of atlas.ICC r (Intracalcarine Cortex Right)
- 187 voxels covering 36% of atlas.Cuneal l (Cuneal Cortex Left)
- 176 voxels covering 27% of atlas.Cuneal r (Cuneal Cortex Right)
- 92 voxels covering 10% of atlas.OFusG l (Occipital Fusiform Gyrus Left)
- 61 voxels covering 1% of atlas.Precuneous (Precuneous Cortex)
- 61 voxels covering 43% of atlas.SCC r (Supracalcarine Cortex Right)
- 47 voxels covering 7% of atlas.TO FusC l (Temporal Occipital Fusiform Cortex Left)
33 voxels covering 45% of atlas.SCC (Suprachalcarine Cortex Left)
23 voxels covering 3% of atlas.TO.FusC (Temporal Occipital Fusiform Cortex Right)
17 voxels covering 1% of atlas.OP (Occipital Pole Right)
17 voxels covering 1% of atlas.OP (Occipital Pole Left)
11 voxels covering 0% of atlas.sLOC (Lateral Occipital Cortex, superior division Right)
8 voxels covering 1% of atlas.Cereb45 (Cerebelum 4 5 Right)
1 voxels covering 0% of atlas.pPaHC (Parahippocampal Gyrus, posterior division Right)
1 voxels covering 0% of atlas.OFusG (Occipital Fusiform Gyrus Right)
663 voxels covering 0% of atlas.not-labeled

Improvisational > MMT:

Clusters (x,y,z) size size p-FWE size p-FDR size p-unc peak p-FWE peak p-unc
-08 -78 +14 7237 0.000000 0.000000 0.000000 0.100736 0.000002

Cluster Atlas Locations:
981 voxels covering 57% of atlas.LG (Lingual Gyrus Right)
770 voxels covering 51% of atlas.LG (Lingual Gyrus Left)
729 voxels covering 15% of atlas.sLOC (Lateral Occipital Cortex, superior division Left)
566 voxels covering 75% of atlas.ICC (Intracalcarine Cortex Right)
535 voxels covering 86% of atlas.ICC (Intracalcarine Cortex Left)
357 voxels covering 56% of atlas.Cuneal (Cuneal Cortex Right)
349 voxels covering 67% of atlas.Cuneal (Cuneal Cortex Left)
289 voxels covering 44% of atlas.TO.FusC (Temporal Occipital Fusiform Cortex Left)
254 voxels covering 5% of atlas.sLOC (Lateral Occipital Cortex, superior division Right)
197 voxels covering 4% of atlas.IOC (Occipital Cortex, inferior division Right)
153 voxels covering 7% of atlas.iLOC (Lateral Occipital Cortex, inferior division Left)
140 voxels covering 15% of atlas.OFusG (Occipital Fusiform Gyrus Left)
95 voxels covering 66% of atlas.SCC (Suprachalcarine Cortex Right)
88 voxels covering 3% of atlas.OP (Occipital Pole Left)
73 voxels covering 4% of atlas.iLOC (Lateral Occipital Cortex, inferior division Right)
70 voxels covering 3% of atlas.OP (Occipital Pole Right)
66 voxels covering 6% of atlas.TO.FusC (Temporal Occipital Fusiform Cortex Right)
42 voxels covering 58% of atlas.SCC (Suprachalcarine Cortex Left)
19 voxels covering 1% of atlas.Cereb6 (Cerebelum 6 Left)
11 voxels covering 3% of atlas.pPaHC (Parahippocampal Gyrus, posterior division Right)
10 voxels covering 2% of atlas.Cereb45 (Cerebelum 4 5 Right)
6 voxels covering 0% of atlas.Cereb6 (Cerebelum 6 Right)
5 voxels covering 1% of atlas.OFusG (Occipital Fusiform Gyrus Right)
4 voxels covering 0% of atlas.PC (Cingulate Gyrus, posterior division)
4 voxels covering 0% of atlas.pTFusC (Temporal Fusiform Cortex, posterior division Left)
4 voxels covering 1% of atlas.Hippocampus r
3 voxels covering 0% of atlas.Ver45 (Vermis 4 5)
2 voxels covering 0% of atlas.toITG (Inferior Temporal Gyrus, temporooccipital part Left)
2 voxels covering 1% of atlas.Ver6 (Vermis 6)
1 voxels covering 0% of atlas.pPaHC (Parahippocampal Gyrus, posterior division Left)
1414 voxels covering 0% of atlas.not-labeled
Right Posterior Parietal Cortex Seeded Connectivity:
Main Effect of Group:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
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</table>

Cluster Atlas Locations:
- 292 voxels covering 19% of atlas.LG l (Lingual Gyrus Left)
- 257 voxels covering 40% of atlas.ICC l (Intracalcarine Cortex Left)
- 193 voxels covering 26% of atlas.ICC r (Intracalcarine Cortex Right)
- 169 voxels covering 3% of atlas.sLOC l (Lateral Occipital Cortex, superior division Left)
- 91 voxels covering 2% of atlas.Precuneous (Precuneous Cortex)
- 86 voxels covering 5% of atlas.LG r (Lingual Gyrus Right)
- 46 voxels covering 5% of atlas.OFusG l (Occipital Fusiform Gyrus Left)
- 41 voxels covering 3% of atlas.Cereb6 l (Cerebelum 6 Left)
- 40 voxels covering 6% of atlas.TO fusC l (Temporal Occipital Fusiform Cortex Left)
- 14 voxels covering 3% of atlas.Cuneal l (Cuneal Cortex Left)
- 14 voxels covering 19% of atlas.SCC l (Supracalcarine Cortex Left)
- 1 voxels covering 1% of atlas.SCC r (Supracalcarine Cortex Right)
- 159 voxels covering 0% of atlas.not-labeled

Improvisational > MMT:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
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Cluster Atlas Locations:
- 574 voxels covering 38% of atlas.LG l (Lingual Gyrus Left)
- 540 voxels covering 31% of atlas.LG r (Lingual Gyrus Right)
- 423 voxels covering 66% of atlas.ICC l (Intracalcarine Cortex Left)
- 380 voxels covering 51% of atlas.ICC r (Intracalcarine Cortex Right)
- 276 voxels covering 6% of atlas.sLOC l (Lateral Occipital Cortex, superior division Left)
- 211 voxels covering 4% of atlas.Precuneous (Precuneous Cortex)
- 164 voxels covering 26% of atlas.Cuneal r (Cuneal Cortex Right)
- 159 voxels covering 24% of atlas.TO fusC l (Temporal Occipital Fusiform Cortex Left)
- 100 voxels covering 11% of atlas.OFusG l (Occipital Fusiform Gyrus Left)
- 82 voxels covering 16% of atlas.Cuneal l (Cuneal Cortex Left)
- 59 voxels covering 5% of atlas.Cereb6 l (Cerebelum 6 Left)
- 40 voxels covering 55% of atlas.SCC l (Supracalcarine Cortex Left)
- 36 voxels covering 25% of atlas.SCC r (Supracalcarine Cortex Right)
- 28 voxels covering 1% of atlas.sLOC r (Lateral Occipital Cortex, superior division Right)
- 18 voxels covering 1% of atlas.OP r (Occipital Pole Right)
- 8 voxels covering 1% of atlas.OFusG r (Occipital Fusiform Gyrus Right)
- 2 voxels covering 0% of atlas.OP l (Occipital Pole Left)
- 2 voxels covering 0% of atlas.Ver45 (Vermis 4 5)
- 547 voxels covering 0% of atlas.not-labeled

DMN ICA Component:

Improvisational > MMT:

<table>
<thead>
<tr>
<th>Clusters (x,y,z)</th>
<th>size</th>
<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
<th>peak p-FWE</th>
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<table>
<thead>
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<th>size p-FWE</th>
<th>size p-FDR</th>
<th>size p-unc</th>
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<tr>
<td></td>
<td>Cluster Atlas Locations: 199 voxels covering 2% of atlas.FP r (Frontal Pole Right) 20 voxels covering 0% of atlas.not-labeled</td>
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<tr>
<td></td>
<td>ImprovMusTrain &gt; GenMusTrain: Clusters (x,y,z)</td>
<td>size</td>
<td>size p-FWE</td>
<td>size p-FDR</td>
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<td>Cluster Atlas Locations: 174 voxels covering 2% of atlas.FP r (Frontal Pole Right) 69 voxels covering 2% of atlas.MidFG l (Middle Frontal Gyrus Left) 45 voxels covering 6% of atlas.IFG oper l (Inferior Frontal Gyrus, pars opercularis Left) 5 voxels covering 0% of atlas.PreCG l (Precentral Gyrus Left) 74 voxels covering 0% of atlas.not-labeled</td>
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References


